Individual behavioral rules sustain the cell allocation pattern in the combs of honey bee colonies (*Apis mellifera*)

Kathryn J. Montovan[a], Nathaniel Karst[b], Laura E. Jones[c], Thomas D. Seeley[d]

[a]*Center for Applied Mathematics, Cornell University, Ithaca, New York*
[b]*Mathematics and Science Division, Babson College, Wellesley, Massachusetts*
[c]*Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, New York*
[d]*Department of Neurobiology and Behavior, Cornell University, Ithaca, New York*

Highlights

- We establish behavioral rules that can create and maintain comb allocation patterns.

- Novel metrics quantify the level of pattern formation.

- Sensitivity analysis determines the relative importance of each parameter.

Abstract

In the beeswax combs of honey bees, the cells of brood, pollen, and honey have a consistent spatial pattern which is sustained throughout the life of a colony. This spatial pattern is believed to emerge from simple behavioral rules. Camazine showed that a set of such rules can explain the formation of the allocation pattern starting from an empty comb and proceeding through the first larval gestational period [1] We show that these rules cannot, however, maintain the pattern over longer timeframes, and we propose new, biologically realistic rules that better sustain the observed allocation pattern. We analyze the four resulting models by performing hundreds of simulation runs over many gestational periods and a wide range of parameter values. We develop new metrics for pattern formation and employ them in analyzing pattern retention over each simulation run. Applied to our simulation results, these metrics show that minor changes in the bees' behavioral rules drastically alter the retention of well-formed brood and pollen regions, thus highlighting queen movement rules that remain poorly understood.

1. Introduction

Complex collective structures are known to arise from simple individual behaviors in a variety of social organisms [2, 1, 3]. Many social insects build large and complex nests arising from the interactions among many individuals [4, 5, 6, 7, 2]. In this paper we build upon work done by Camazine to show that the spatial pattern of comb cell use in honey bee (*Apis mellifera*) nests can arise from the individual actions of thousands of bees and also be maintained by a single set of simple behavioral rules [1]. The pattern has been well studied [8, 1] and is thought to be important to the efficient function of a colony.

Our primary goal is to explain how simple, biologically relevant rules produce sustained patterns in the storage locations of brood, honey and pollen within a honey bee colonys nest. The nest consists of parallel combs made up of hexagonal cells that are filled with either brood, honey, or pollen. In nature, brood cells are typically concentrated in a roughly circular region near the center of a comb. A ring of cells used for pollen storage typically surrounds this brood region. The remainder of the cells are filled with honey. Figure 1 shows this general pattern. Brood develop and vacate their cells after 21 days, and although honey or pollen is occasionally placed in these

evacuated cells, they are quickly emptied and filled with brood [1]. This cell allocation pattern is maintained throughout the entire life of the colony (years) despite a comparatively short lifespan of workers (weeks) and occupancy period for brood cells (21 days) [9].

The observed arrangement of the cells has several distinct benefits. Controlled temperatures are necessary for brood survival [10, 11], and it is believed that concentrating brood cells in the center of the comb effectively insulates the larvae from fluctuating environmental conditions [12]. Cells near the edge of the comb are often distorted, and as a result can be problematic for successfully rearing brood [8]. In addition, the primary consumers of pollen are the nurse bees feeding the brood [13], so storing pollen near the brood reduces the time and energy spent by nurse bees in consuming stored pollen [9].

Camazine explained how the combined individual actions of thousands of workers could form the observed pattern using simple, biologically relevant rules but did not explain how the pattern was maintained throughout the life of the colony [1]. Before his work, it was commonly believed that the pattern arose because each bee followed an internal blueprint, placing each product in its associated cells according to an overall plan [8, 10, 14, 1]. Camazine showed experimentally that this is not the case by placing empty comb into the brood region. He observed that initially this comb was filled with both pollen and honey, but that fairly quickly the cells in the comb were emptied and filled with brood [1]. Camazine argued that this pattern can arise from a specific combination of elementary behaviors that dictate how the queen chooses brood cells, how cells are chosen for storing new pollen and honey, and how cells are chosen for honey and pollen consumption [9]. However, he did not look at what happened beyond the first 21 days when evacuation of brood cells begins. Simplified differential equations models have helped explain the importance of parameter values on pattern formation [12, 15], but these models are also limited to the first 21 days of pattern formation and they ignore the effects of adult bees emerging from the comb. We begin by reviewing the Camazine model and its associated behavioral rules before we explain our modifications that can maintain the cell allocation pattern beyond the first 21 days [1].

Queen Movement. The queen moves over the comb, selecting suitable cells into which she inserts eggs. She starts in the center of the comb and performs a random walk, at each step moving one cell in a (uniformly) random direction. The queen deposits at most 60 eggs per hour in cells that are

3

both currently empty and at most four cell lengths away from the nearest brood cell. This occurs 24 hours a day. Brood cells remain filled for 21 days before being vacated and then refilled.

Honey and Pollen Deposition. When flowers are in bloom and weather conditions are favorable, foraging bees bring home honey and pollen to store in the comb. The honey and pollen are deposited in cells (uniformly) randomly selected from all comb cells. If the chosen cell is either empty or partially filled with the same substance as the one being deposited, then the honey/pollen is added. The exact manner in which cells are chosen for honey and pollen deposition and consumption is unclear in the original Camazine model [1]. It is known that Pollen foragers and honey storers examine multiple cells when depositing loads of food [16, 17] and that they deposit less honey and pollen when the comb is full [16]. To be consistent with these observations, we chose to allow 6 attempts to find a suitable cell which creates the desired decreased deposition rate for full combs but a good chance of finding a suitable cell in an emptier comb. This interpretation conforms to the descriptions in Camazine [9]. Deposition only occurs during daylight hours, 12 hours per day. Full cells contain 20 loads of pollen or honey. The ratio of pollen input to honey input is varied over the season with an average of 0.2.

Honey and Pollen Consumption. Honey and pollen are removed when the worker bee or nurse bee chooses a cell (uniformly) randomly from all comb cells and removes honey/pollen if it is present. Six attempts to find a suitable cell are allowed as described above. To account for additional removal of honey/pollen from cells adjacent to brood cells, the amount removed is linearly proportional to the number of adjacent brood cells, $1 + 9(n/9)$, where n is the number of adjacent brood cells (out of nine since the model uses a square grid). The average ratios of removal to input are 0.6 for honey and 0.95 for pollen.

The model using just these three rules will form the desired cell allocation structure for a single brood cycle. Preferential honey and pollen consumption near brood empties these cells more quickly. These emptied cells are often filled with brood and pollen because the queen only oviposits into cells that are near current brood cells and the turnover of pollen is much quicker than that of honey [1]. These rules explain the creation of the storage pattern, however, they cannot sustain the allocation pattern once evacuation of brood cells begins (see Figure 2).

In this paper we go beyond pattern formation and present novel alterna-

tives to the above rules that are able to maintain the comb pattern through multiple brood cycles over a wide range of parameter values.

2. Methods

Consider a comb that starts with a well-formed pattern. Through time, the actions of the colony can either maintain or destroy this pattern. The difference between maintenance and destruction lies in the choice of parameters for key functions, as well as in implementation choices for important pieces of the model. We have already noted that the Camazine model [9] forms the pattern when starting from an empty comb, but that this pattern breaks down after the first cohort of new bees starts to vacate the brood cells. We propose two modifications to Camazine's model (Model 1) as outlined below.

Alternate Queen Movement. The queen's walk is biased towards the center of the comb in a way in which her chosen direction is nearly uniformly random when she is at the center but becomes increasingly biased back toward the center as her distance from the center increases. For this purpose we use a Gaussian distribution of directions with a mean toward the center of the comb and a standard deviation of $\pi(1 - d/d_{max})$, where d is the distance to the center of the comb, and d_{max} is the maximum distance from any cell to the center of the comb. Angles that are outside $[0, 2\pi)$ are taken modulo 2π. This results in a distribution with each edge cell receiving roughly half as many visits as each cell near the center of the comb. These modifications are relatively minor and biologically justifiable because of temperature gradients in the nest that might guide the queen's movements away from the edges of the comb. When the comb is empty, the bees concentrate their energy on maintaining an elevated temperature in the central part of the comb, thus creating a temperature gradient with a hot spot that is away from the edges. When the comb is full, as will be the case for most of our modeling, there is a well established temperature gradient from center to edge [18].

Alternate Honey/Pollen Consumption. Honey and pollen are removed from randomly selected cells with the probability of selecting a particular cell that is linearly proportional to the number of brood cells within a chosen distance. The probability that a specific cell is chosen is $1 + A(t-1)$ where A is the fraction of cells in the desired neighborhood that contain brood (excluding the cell in question), and t is a parameter defining the rela-

tive probability of choosing a cell completely surrounded by brood compared with those that have no brood neighbors. This captures the idea of nurse bees taking more honey/pollen from cells near brood without assuming that the nurse bees take multiple trips from the same cell. Cells completely surrounded by brood are t times more likely to be chosen than those with no brood neighbors.

The alternate honey/pollen consumption method represents an adjustment in implementation only. The underlying idea remains the same: if a significant amount of the consumed honey and pollen are used for rearing brood, then storage cells near brood will be emptied more quickly. This modification is biologically plausible since a nurse bee can only remove one load of pollen or honey at a time regardless where the honey/pollen is located. Moreover, there is no evidence that nurse bees track the locations of honey/pollen cells, and the act of leaving the brood area in search of nectar/pollen causes nearby storage cells to be encountered more often than those farther away from brood cells.

The alternate model parts are tested using four models. The first, Model 1, is the original Camazine model as outlined in the introduction [1, 9]. In Model 2, the alternate queen movement method is employed while leaving the remaining rules identical to those of Model 1. Model 3 uses the alternate honey/pollen consumption rules and leaves all other rules identical to those of Model 1. Model 4 employs the alternate methods of both queen movement and honey/pollen consumption. Model parameter values were varied over a wider range than were used in [1] so that the sensitivity of the model to choices of parameter values could be assessed.

2.1. Model implementation

We implement the four models using numerical simulations. All models were tested with 200 runs of 120 days simulated over the parameter ranges described in A.1. The exact parameters for each run were determined by Latin hypercube sampling [19, 20]. This method chooses 200 equally likely values for each parameter and then randomly selects (without replacement) from these values to create a unique parameter set for each of the model runs. In order to compare each model's ability to maintain the pattern, each simulation begins with an ideal comb pattern of a center region of brood, surrounded by a ring of pollen, and honey in all remaining cells. The assignment of type to each cell is deterministic and constant across all simulations (see Figure 1). Each storage cell has the potential to contain

6

0 to 20 loads of honey or pollen, with the initial amount chosen uniformly randomly from this range. Similarly, the initial age of brood cells is chosen uniformly randomly from 1 day to 21 days.

The modeled comb is a rectangle with dimensions 45 cells by 75 cells. We chose to use square cells because they were easier computationally and because the difference in simulation results between the two structures was not noticeable. This gives each cell eight neighbors instead of the six that would be expected for hexagonal cells. During the 12 hours of daylight honey and pollen are deposited in the cells and at all hours honey and pollen are consumed. Also at all hours, the queen travels around the nest laying eggs into suitable cells. We chose to let these events happen in random order to be more realistic and to remove any bias caused by continually implementing one process before another. At the end of each hour, a fraction of the 21-day-old immature bees vacate their cells (chosen randomly from all 21-day-old immatures), and by the end of the day all 21-day-old, immatures have vacated their cells. Temporal variability in maximum honey/pollen collection occurs in one of three possible ways: uniform, uniform random and clumped according to a Markov process.

2.2. Brood and Pollen Ring metrics

To assess the level of pattern retention during the simulation runs, we developed two metrics that describe the compactness of the brood region and the level of definition of the pollen ring (or gap of empty cells). The brood metric is the average number of brood neighbors for each brood cell. We observed qualitatively that in simulations with brood compactness metric of seven or higher, the brood cells are sufficiently dense to fit the observed pattern. The pollen metric is the average distance from each honey cell to the nearest brood cell. In this case we observed that pollen metric of nine or more indicates a well-formed pollen ring, i.e., one that forms a strong separation of honey cells from brood cells. In combination, these two metrics accurately describe how well the allocation adheres to the desired pattern. These metrics are used to assess the sensitivity in the model predictions over a range of reasonable parameter values.

3. Results and Discussion

Our modeling framework contains the same general pattern formation processes that Camazine described [1], but to check that our models would

in fact create the initial pattern of a compact brood region surrounded by a ring of pollen, we performed simulations of all four models for the first twenty days. For Model 1, the Camazine model, our simulations reproduced Camazine's results [1]. As is shown in Figure 2, the desired pattern forms during the first twenty days of simulation but gradually dissolves as brood cells are vacated. We found that all of the models were able to form the initial pattern for a range of parameter values. Figure 3 shows one such simulation for Model 4. The initial pattern is not perfect, but the compact brood region forms and the pollen ring is visible. While Models 1 and 4 form similar patterns initially, Model 1 cannot maintain the pattern. Model 4 is able to both create and maintain the pattern.

To examine which model and parameter combinations retain the desired cell allocation pattern, we began simulations on day 0 with the same ideal starting structure (Fig. 2). The amount of honey/pollen and age of brood are assigned randomly to each cell. In this way, the simulations focused on whether the desired pattern was maintained, not just initially formed. The rest of the simulations started with this ideal pattern. Figure 4 shows a series of snapshots demonstrating each model's ability to maintain the desired pattern.

The overall differences between the four models in the ability to maintain a compact brood region and clear pollen ring over time are apparent in the trajectories of the brood and pollen metrics. Figure 5 shows how these metrics evolve through the 120 days of simulation for each of the four models. Simulations were performed for 200 parameter combinations for each model but only the 20 with the highest brood and pollen metrics are shown in Figure 5. One can see that changing the honey/pollen consumption rule in Model 3 allows retention of the pollen ring for 120 days in some simulations. Biasing the random walk of the queen towards the center of the frame in Model 2 slightly improved maintenance of the brood region, but none of the runs of Model 2 maintained high pollen metrics. Combining these modifications in Model 4, we found a large number of parameter combinations sustained both a dense brood region and a nicely formed ring of pollen or empty cells. None of the parameter combinations for Models 1 and 2 resulted in pattern retention past day 20. By contrast, we found 3 and 27 parameter combinations for which Models 3 and 4, respectively, sustained the desired pattern over multiple brood cycles.

Given the stochastic nature of the simulation, there is the natural question as to whether a given simulation of a particular parameter combination is

representative of the behavior in general. Figure 6 shows metric traces for 20 simulations of one parameter combination applied to Model 4. The traces of both metrics are relatively tight, and in particular, all traces are qualitatively similar in that all exceed the metric thresholds most of the time. All brood metrics were within 15% of the mean, and all pollen ring metrics were within 5% of the mean.

3.1. Sensitivity testing

We performed sensitivity analyses to compare the effects of different parameters on model outcome. Because our parameter estimates (A.1) are relatively uncertain, though biologically reasonable, we considered the effects of parameter variations across the multidimensional hypercube used for parameter determination [21, 19]. As described earlier, we employed a grid of 200 evenly spaced values for each parameter, which produced 200 randomly generated parameter sets for the model. For each parameter set, we began simulations on day 0 with an initial ideal starting structure (Figure 1) and then simulated the model for 120 days. Model metrics were then computed for days 10-60, and the values averaged. The relative importance of each parameter to model outcome was determined via multiple regression of each model metric (brood clumping and pollen ring formation) on parameter values.

Both the brood clumping and pollen ring metrics are particularly sensitive to variations in parameters governing how quickly the comb fills. Results summarized in Figure 7 suggest that brood clumping is strongly affected by the queens cell visitation rate (n) and the factors that influence the honey and pollen stores in the comb (r_h, r_p). Pollen ring formation and maintenance is also strongly affected by these parameters, as well as by the quality of pollen and nectar availability, N_{type} (see A.1 for details). Somewhat counterintuitively, for the parameter ranges tested, brood clumping and pollen ring formation are relatively insensitive to the amounts of honey collected per day w, as well as the ratio of pollen to honey deposited in the comb, ρ_{ph}.

4. Conclusion

Camazine showed that the distinctive cell allocation pattern observed in the combs of honey bee nests can be produced with just a few biologically realistic rules of behavior [9]. The ability of Camazine's rules to accurately capture the formation of this pattern is promising support for the presence

9

of self-organization in this system. However, we show that pattern retention after one brood cycle requires slightly different rules. We propose altering the movement rule of the queen and adjusting the honey/pollen consumption rules. Both adjustments invoke biologically plausible mechanisms. We show through simulations that the addition of these alterations to the Camazine model allows for pattern retention over multiple brood cycles. These findings are demonstrated in the performance of novel metrics that quantify and identify the presence of the desired cell allocation pattern. Additionally, the new model is able to form the initial comb pattern on an empty comb over a range of parameter values, and to maintain the pattern over multiple brood cycles.

Our work suggests a need for additional experimental research on the movement of the queen across the comb. Studies of the temperature gradients across the comb and the associated queen movement and oviposition are needed to determine whether the queen is performing a biased random walk and whether temperature gradients inform her movement decisions. The confirmation or refutation of the assumptions of the models presented in this work will be important steps toward understanding the remarkable collective behaviors of honey bees.

Disclosure Statement:

None of the authors had any actual or potential conflicts of interest.

Acknowledgments

5. References

References

[1] S. Camazine, Self-organizing pattern formation on the combs of honey bee colonies, Behavioral Ecology and Sociobiology 28 (1) (1991) 61–76.

[2] E. Bonabeau, G. Theraulaz, J. Deneubourg, N. R. Franks, O. Rafelsberger, J. Joly, S. Blanco, A model for the emergence of pillars, walls

and royal chambers in termite nests, Philosophical Transactions of the Royal Society B: Biological Sciences 353 (1375) (1998) 1561–1576.

[3] G. G. Theraulaz, J. J. Gautrais, S. S. Camazine, J.-L. J. Deneubourg, The formation of spatial patterns in social insects: from simple behaviours to complex structures., Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences 361 (1807) (2003) 1263–1282.

[4] J. M. Pasteels, J. L. Deneubourg, S. Goss, Self-organization mechanisms in ant societies (I): trail recruitment to newly discovered food sources, in: J. M. Pasteels, J. Deneubourg (Eds.), From Individual to Collective Behavior in Social Insects: Les Treilles Workshop, Birkhauser, 1987, pp. 155–175.

[5] N. R. Franks, N. Gomez, S. Goss, J. L. Deneubourg, The blind leading the blind in army ant raid patterns: Testing a model of self-organization (Hymenoptera: Formicidae), Journal of Insect Behavior 4 (5) (1991) 583–607.

[6] T. D. Seeley, S. Camazine, J. Sneyd, Collective decision-making in honey bees: how colonies choose among nectar sources, Behavioral Ecology and Sociobiology 28 (4).

[7] N. R. Franks, A. Wilby, B. W. Silverman, C. Tofts, Self-organizing nest construction in ants: sophisticated building by blind bulldozing, Animal behaviour 44 (1992) 357–375.

[8] T. D. Seeley, R. A. Morse, The nest of the honey bee (Apis mellifera L.), Insectes Sociaux 23 (4) (1976) 495–512.

[9] S. Camazine, J. Deneubourg, N. Franks, J. Sneyd, G. Theraulaz, E. Bonabeau, Self-Organization in Biological Systems , Princeton studies in complexity, Princeton University Press, 2001.

[10] T. D. Seeley, The ecology of temperate and tropical honeybee societies, American Scientist 71 (3) (1983) 264–272.

[11] J. J. Tautz, S. S. Maier, C. C. Groh, W. W. Rossler, A. A. Brockmann, Behavioral performance in adult honey bees is influenced by the temperature experienced during their pupal development., PNAS 100 (12) (2003) 7343–7347.

[12] S. Camazine, J. Sneyd, M. J. Jenkins, J. D. Murray, A mathematical model of self-organized pattern formation on the combs of honeybee colonies, Journal of Theoretical Biology 147 (4) (1990) 553–571.

[13] K. Crailsheim, L. Schneider, N. Hrassnigg, G. Buhlmann, U. Brosch, R. Gmeinbauer, B. Schoffmann, Pollen consumption and utilization in worker honeybees (Apis mellifera carnica): Dependence on individual age and function, Journal of Insect Physiology 38 (6) (1992) 409–419.

[14] M. L. Winston, The biology of the honey bee, Harvard Univ Pr, 1987.

[15] M. J. Jenkins, J. Sneyd, S. Camazine, J. D. Murray, On a simplified model for pattern formation in honey bee colonies, Journal of Mathematical Biology 30 (3) (1992) 281–306.

[16] T. D. Seeley, Social foraging in honey bees: how nectar foragers assess their colony's nutritional status, Behavioral Ecology and Sociobiology 24 (3) (1989) 181–199.

[17] N. Calderone, B. Johnson, The within-nest behaviour of honeybee pollen foragers in colonies with a high or low need for pollen, Animal behaviour (63) (2002) 749–758.

[18] F. Kronenberg, H. C. Heller, Colonial thermoregulation in honey bees (Apis mellifera), Journal of Comparative Physiology B 148 (1) (1982) 65–76.

[19] S. M. Blower, H. Dowlatabadi, Sensitivity and Uncertainty Analysis of Complex Models of Disease Transmission: An HIV Model, as an Example, International Statistical Review 62 (2) (1994) 229–243.

[20] S. P. Ellner, J. Guckenheimer, Dynamic Models in Biology, 1st Edition, Princeton University Press, 2006.

[21] M. D. McKay, Latin hypercube sampling as a tool in uncertainty analysis of computer models, in: Proceedings of the 24th conference on Winter simulation, WSC '92, ACM, New York, NY, USA, 1992, pp. 557–564.

[22] W. J. Nolan, The brood-rearing cycle of the honeybee (Department bulletin / United States Department of Agriculture), U.S. Dept. of Agriculture, 1925.

[23] F. S. Bodenheimer, Studies in animal populations II: seasonal population-trends of the honey-bee, The Quarterly Review of Biology 12 (4) (1937) 406–425.

Appendix A. Parameter ranges

Because the estimates are all somewhat speculative, we consider a wide range of parameter values in exploring model behavior. Ranges for the key parameters in the model were chosen as follows, with all ranges extended to test the sensitivity of the model to each parameter.

n The number of cells visited by the queen in one hour is estimated from the recorded number of eggs laid per hour. The queen lays between 1000 and 2000 eggs in a day, with is equivalent to 42-84 eggs per hour [22, 23, 1]. We selected a range from 60-120 cells visited per hour because many attempts to lay eggs fail either because the cell is already in use or because it is too far from the nearest brood cell. In an empty frame the queen will lay roughly the desired maximum number of eggs and in a more full comb her efficiency decreases.

r_b The maximum distance that a queen will oviposit from an existing brood cell (r_b) is based on the Camazine model assumption that $r_b = 4$, but the range has been extended to include shorter distances (1-4).

r_n The maximum distance, r_n, from the nearest brood cell at which honey and pollen consumption is increased due to the proximity of brood cells was extended from Camazine's assumption of radius $r_n = 1$ in the original model to a wider range $(1 - 4)$.

w The average number of loads of honey gathered per day (w) was derived from 60 kg of honey entering the hive in a season, 40 mg of honey in each load, 150 days in the summer season, and approximately 12 hours per day for honey/pollen collection [1, 9]. This results in approximately 833 loads per hour during the daytime. This estimate was then increased to account for the fact that not all attempts to deposit honey are successful, and a range of values (1000-4000) were investigated.

r_{ph} The ratio of average loads of pollen to average loads of honey deposited in the comb daily, r_{ph} has been observed to be about 0.26 [1], with the range extended to $(0.2-1)$.

ρ_p, ρ_h The ratios of pollen and honey consumption to collection (ρ_p and ρ_h, respectively) were chosen to be in the range of $0.9 - 1.1$ since our interest is in the sustenance of the pattern after the comb fills. This is realistic because of certain mechanisms that ensure that the colony does not bring in too much honey/pollen for its storage capacity, which include comb building and colony splitting to create a new colony.

N_{type} The temporal pattern of nectar and pollen deposition are modeled in three possible ways: uniform constant ($N_{type} = 0$), uniform random ($N_{type} = 1$), and Markov clumped random ($N_{type} = 2$). The mean daily amount is the same for all three processes. These three possibilities represent a range from simplified (uniform) to more realistic (Markov clumped).

t Ratio of honey/pollen taken from cells fully surrounded by brood cells to honey/pollen taken from cells with no brood neighbors was based on Camazine's estimate of $t = 10$ [1]. The range was extended to $5 - 20$ for sensitivity testing.

Table and Figure Captions

Figure 1 The general comb pattern with brood (black cells) in the center, the pollen ring (dark gray cells) surrounding the brood region and honey (light gray cells) in the periphery. When empty cells are present they will be shown in white. (Note: there are no empty cells in this example).

Figure 2 Snapshots of a typical simulation of an initially empty comb becoming full and forming the desired pattern over the first 20 days. Notice that after the brood begin to vacate their cells at day 21, the pattern is not maintained.

Figure 3 A sample simulation run of Model 4 starting from an empty comb. The pattern is roughly formed over the first 20 days and is retained past day 20 as the brood begin to vacate their cells.

Figure 4 Snapshots of the comb patterns in simulation runs of the four models. These runs were chosen because they resulted in the highest pattern metrics out of all parameter combinations for each model. Models 1 (Camazine model) and 2 (Alt. Queen Movement) had no combinations resulting in a satisfactorily maintained allocation pattern. Models 3 (Alt. Consumption) and 4 (Alt. Queen Movement and Consumption) both had multiple (3 and 27 respectively) parameter combinations with the pattern sustained over the first 40 days.

Figure 5 Trajectories of the two metrics of interest for the twenty best parameter combinations for each of the four models. Recall that if the brood clumping metric is above seven and the pollen ring metric is above nine, then the pattern is considered to be well formed. Combining the modifications in honey/pollen consumption and queen movement in Model 4 resulted in a significant range of parameter combinations that have the ability to maintain a well-formed pattern over 40 days.

Figure 6 Trajectories of the two metrics of interest for twenty simulations of one specific parameter combination applied to Model 4.

Figure 7 Sensitivities of the Model 4 brood and pollen metrics to parameter variation. The metrics were averaged over days 10 to 60. See Table A.1 for parameter definitions and ranges.
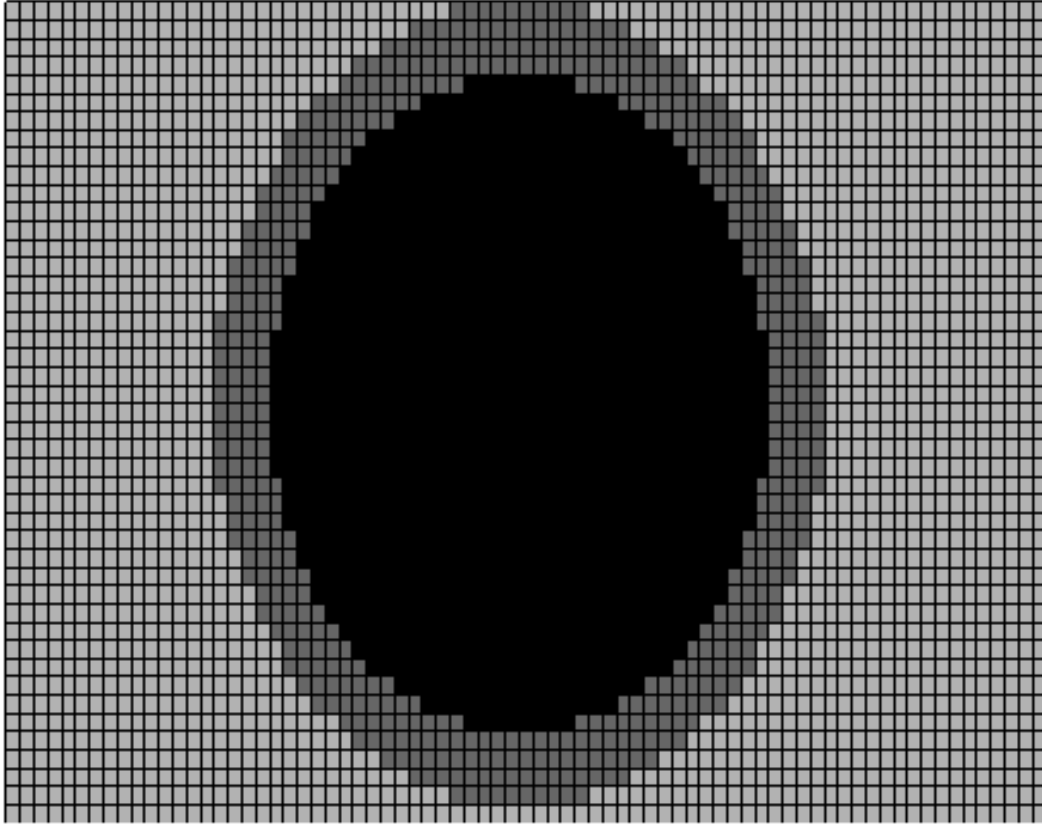
Figure A.1: The general comb pattern with brood (black cells) in the center, the pollen ring (dark gray cells) surrounding the brood region and honey (light gray cells) in the periphery. When empty cells are present they will be shown in white. (Note: there are no empty cells in this example).
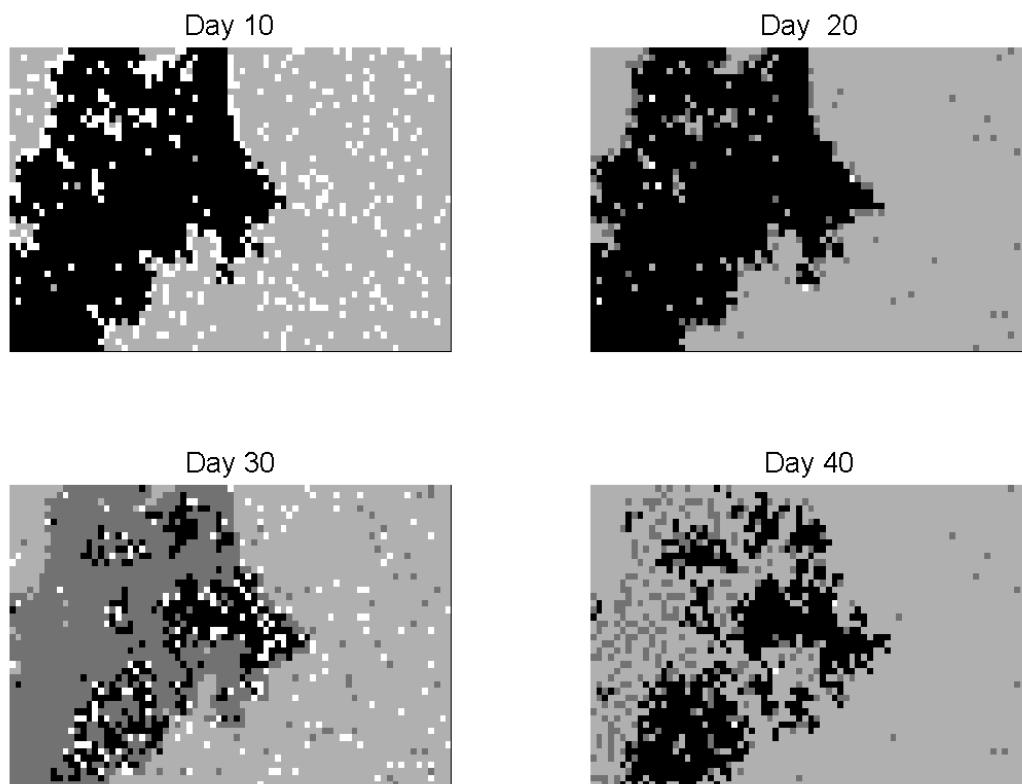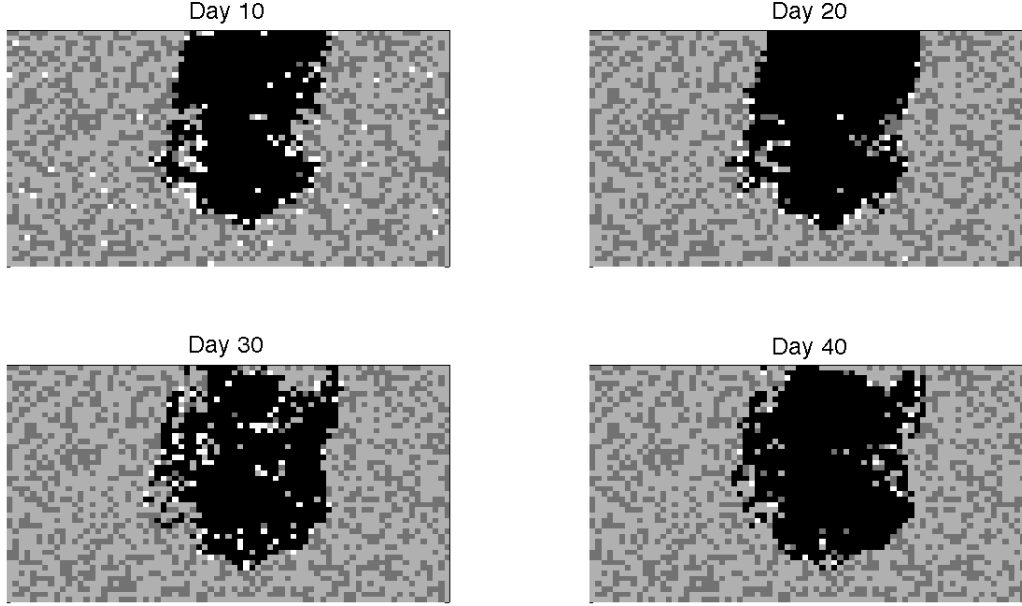
Figure A.2: Snapshots of a typical simulation of an initially empty comb becoming full and forming the desired pattern over the first 20 days. Notice that after the brood begin to vacate their cells at day 21, the pattern is not maintained.

Figure A.3: A sample simulation run of Model 4 starting from an empty comb. The pattern is roughly formed over the first 20 days and is retained past day 20 as the brood begin to vacate their cells.

Parameter	Description	Range
n	Queen's cell visitation rate (cells per hour)	$60 - 120$
r_b	Brood requirement radius (cells)	$1 - 4$
r_n	Preferential nectar consumption radius (cells)	$1 - 4$
w	Average honey collection (loads per day)	$1000 - 4000$
r_{ph}	Ratio of pollen collection to honey collection	$0.2 - 1.0$
r_p	Ratio of pollen consumption to pollen collection	$0.9 - 1.1$
r_h	Ratio of honey consumption to honey collection	$0.9 - 1.1$
N_{type}	Temporal distribution of daily nectar and pollen collection: uniform constant ($N_{type} = 0$), uniform random ($N_{type} = 1$) and Markov clumped random ($N_{type} = 2$)	$0 - 2$
t	Ratio of honey/pollen taken from cells fully surround by brood cells to honey/pollen taken from cells with no brood neighbors	$5 - 20$

Table A.1: Parameters used in simulations of Models 1- 4 and the sensitivity analysis.
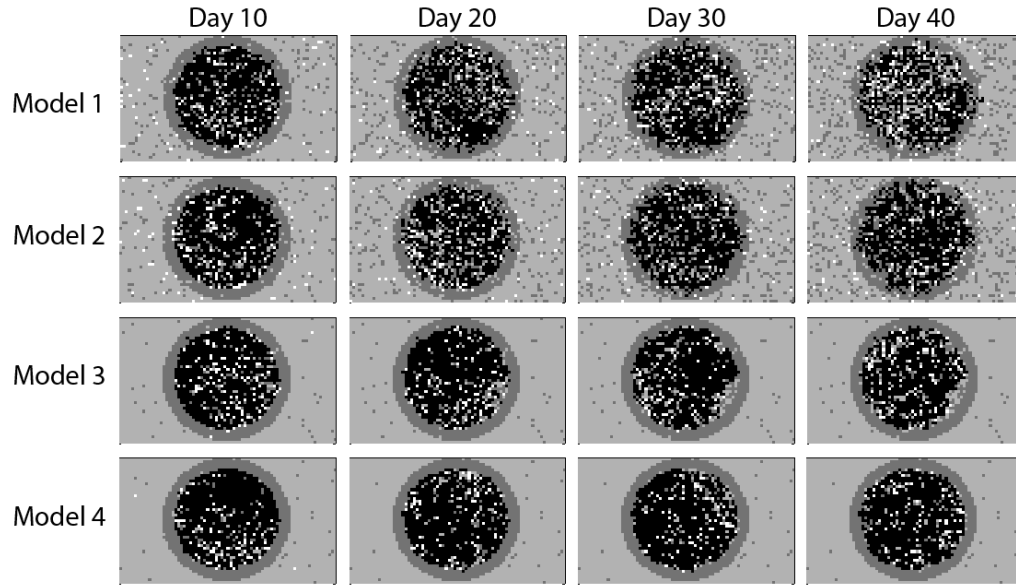
Figure A.4: Snapshots of the comb patterns in simulation runs of the four models. These runs were chosen because they resulted in the highest pattern metrics out of all parameter combinations for each model. Models 1 (Camazine model) and 2 (Alt. Queen Movement) had no combinations resulting in a satisfactorily maintained allocation pattern. Models 3 (Alt. Consumption) and 4 (Alt. Queen Movement and Consumption) both had multiple (3 and 27 respectively) parameter combinations with the pattern sustained over the first 40 days.
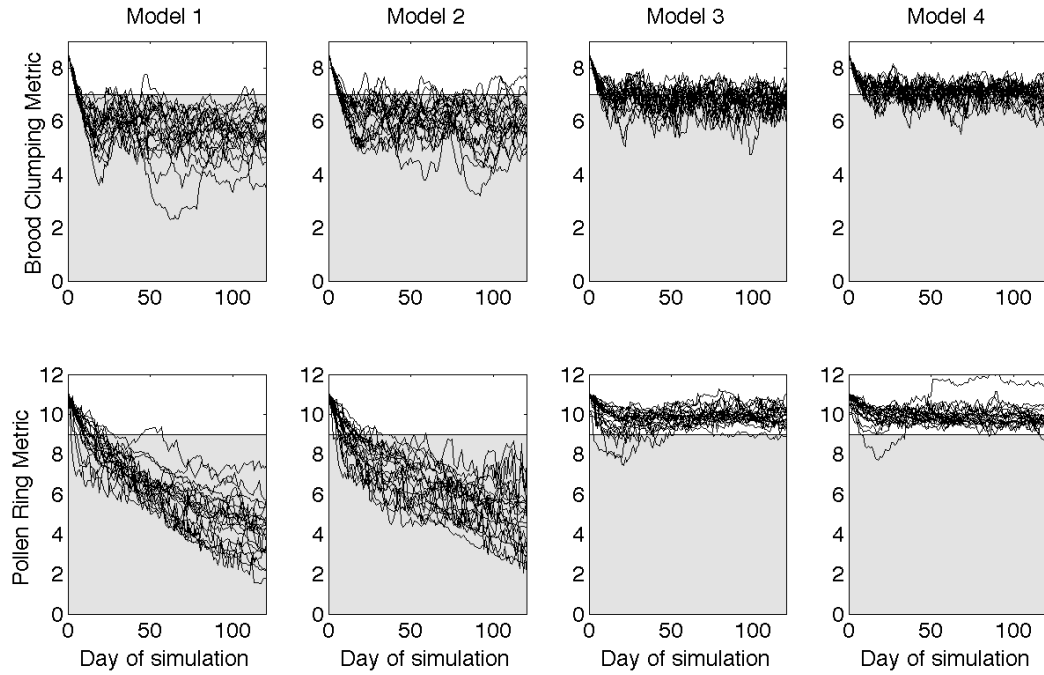
Figure A.5: Trajectories of the two metrics of interest for the twenty best parameter combinations for each of the four models. Recall that if the brood clumping metric is above seven and the pollen ring metric is above nine, then the pattern is considered to be well formed. Combining the modifications in honey/pollen consumption and queen movement in Model 4 resulted in a significant range of parameter combinations that have the ability to maintain a well-formed pattern over 40 days.
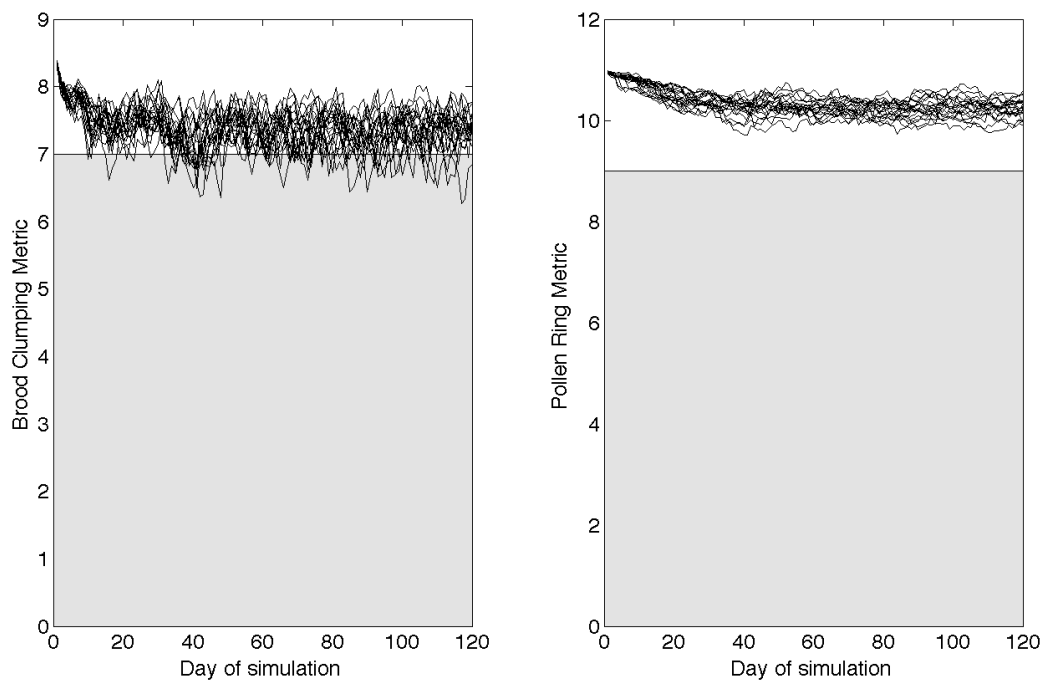
Figure A.6: Trajectories of the two metrics of interest for twenty simulations of one specific parameter combination applied to Model 4.
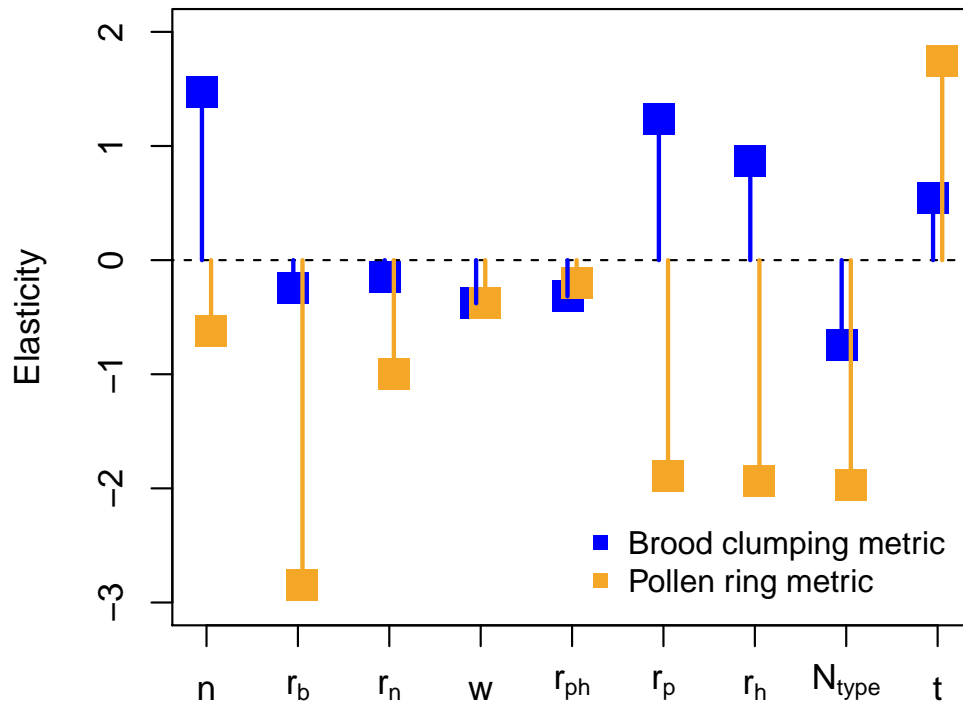
Figure A.7: Sensitivities of the Model 4 brood and pollen metrics to parameter variation. The metrics were averaged over days 10 to 60. See Table A.1 for parameter definitions and ranges.